



# Sexual Selection: Placentation, Superfetation, and Coercive Copulation

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# **Sexual selection: placentation, superfetation, and coercive copulation.**

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**Placentation in poeciliid fishes is associated with conception of overlapping litters and a shift in male mating strategies from less to more coercive. Sperm competition in ovaries of multiply-inseminated females may favor fertilization of immature eggs during ongoing pregnancies.**

Intersexual selection is commonly described as the process by which female choice of mating partners shapes male attributes to conform to female preferences, but it also encompasses male adaptations to circumvent female choice by deceit or coercion. The diverse life histories of fish provide many opportunities for exploring this evolutionary dynamic. External fertilization allows a female substantial control over who sires her fry because she determines when (and near whom) her eggs are released, but non-chosen males of many species adopt opportunistic strategies of darting in to release sperm at the moment a female spawns with a chosen male [1]. Internal fertilization has evolved multiple times, perhaps as an adaptation to preempt sperm of other males by fertilizing eggs before their release. Males gain the additional benefit that they need not wait until females oviposit but can deposit their sperm and leave in search of other females. And males can inseminate without being chosen. Copulation probably began as an assertion of male priorities over female autonomy [2]. A recent study by Pollux *et al.* [3] finds surprising correlates of male mating behavior in guppies and their relatives (poeciliid fishes).

Poeciliid males use an elaborately modified anal fin, a gonopodium, to inject sperm into female gonoducts, and are noted for bright colors, elaborate courtship, and frequent coercive mating [3]. Males of some species (e.g., *Poecilia latipinna* Figure 1a), court females or sneak copulations depending on male genotype and opportunity [4] whereas males of other species (e.g., *Heterandria formosa* Figure 1bc), rely exclusively on unsolicited copulation without prior courtship [5]. Fertilization and embryonic development occur within ovarian follicles, with well-developed offspring released from follicles shortly before birth. The timing of maternal investment varies from species in which eggs are fully provisioned with yolk before fertilization (lecithotrophy) to species

in which mothers transfer substantial nutrients to embryos after fertilization (matrotrophy). Nutrients are transferred across follicular epithelia of both lecithotrophic and matrotrophic mothers but transfer is considered to be 'placental' once follicles contain embryos.

Pollux *et al.* studied associations between placentation and male secondary sexual characters in 94 poeciliid species. Matrotrophy was associated with loss of bright colors and courtship displays, suggesting reduced importance of precopulatory female choice. Matrotrophy was also associated with smaller males with longer gonopodia, traits that enhance male maneuverability and success in rapid copulatory forays. Finally, matrotrophy was associated with superfetation, the presence of multiple broods at different stages of development within individual ovaries. Thus, post-zygotic maternal provisioning is associated with shifts in male behavior from courtship to coercion [3].

The authors propose that matrotrophy and superfetation create opportunities for post-copulatory choice by females and thus lead to a loss of courtship by males [3]. An alternative interpretation reverses the causal arrow: matrotrophy and superfetation are consequences of changes in male behavior. The difference between the hypotheses is expressed in the question, did males abandon courtship and bright colors because females ceased to prefer these traits or did males cease to court because of increased returns from coercion? In other words, did placentation enable a shift in female criteria of choice from pre-copulatory to post-copulatory characters or was placentation an indirect consequence of changes in male behavior that reduced female opportunities of pre-copulatory choice?

Female poeciliids need not remate to replenish sperm after giving birth. Many guppies, in a recent field study, were posthumously fathered by males whose sperm had survived for months in the ovaries of longer-lived females [6]. Thus, sperm from a single mating can survive through multiple pregnancies to sire offspring in multiple litters and ovaries of pregnant females contain resident sperm waiting for eggs to fertilize. In some lecithotrophic poeciliids, the next clutch does not start to fill with yolk until after the birth of the previous litter whereas vitellogenesis in other species commences during

pregnancy with fertilization of a new clutch immediately after birth of the previous litter [7].

Matrotrophy and superfetation may have originated from sperm 'jumping the gun' and fertilizing eggs before they were fully provisioned. Such a strategy could reflect competition among sperm already present in ovaries or be preemptive action of sperm from earlier inseminations to forestall fertilizations by sperm of future inseminations. If a sperm fertilizes an egg before it is fully-yolked and the mother continues to provision its follicle, then the latter stages of provisioning are post-zygotic (matrotrophic) rather than pre-zygotic (lecithotrophic) without a change of maternal physiology. If eggs are fertilized while a mother is pregnant, she carries overlapping litters without any change in the way she provisions follicles (Figure 2). Although superfetation and matrotrophy may have originated from 'premature' fertilization of immature eggs, the expression of these characters in extant species will have been modified by subsequent selection on maternal supply and offspring demand.

These hypotheses do not directly explain why matrotrophy and superfetation should be associated with coercive mating. A possible explanation is that more male investment in coercion results in more intense sperm competition because females are inseminated by more males. The evolution of superfetation is probably also facilitated by selection on females for rapid production of offspring, favoring maturation of the next clutch of oocytes during an ongoing pregnancy. One curious consequence of coercive mating is that it may have facilitated the evolution of female-only lineages (e.g., *Poecilia formosa*, *Poeciliopsis monacha-lucida*) that use sperm from males of related species to sire offspring who pass on their maternal genes only [8]. Copulation with these females is a genetic dead end for males but the need for coercive males to make quick decisions without close inspection may aid their deception by female 'sperm-parasites'.

More than a century ago, Seal described the mating behavior of *Gambusia holbrooki* and *Heterandria formosa* [5]. He wrote that "The males are continually engaged in a pursuit of the females while the females are apparently adverse to sexual dalliance and at all times unwilling participators and quick to resent the advances of the males. I

have never witnessed anything to indicate a reciprocity of desire in coitus it being always a chance touch and go on the part of the males." But he also described males fleeing in terror from the much larger females who would sometimes kill their sexual harassers. He observed that "in the attacks of the females of either species they seem to endeavor to bite the long slender organ of the male, which is no doubt the most vulnerable point." Females are neither behaviorally nor evolutionarily passive.

Consensual mating becomes more attractive for males when female adaptations reduce relative returns from coercion. By this process, mating systems can evolve to be less coercive. Phylogenetic analyses suggest that coercion is ancestral for male poeciliids and that courtship has evolved and been lost multiple times [9]. Females are proposed to obtain genetic benefits from mating with multiple males via post-copulatory choice of which sperm fertilize their eggs or which offspring they provision [10–13]. But males may evolve adaptations to subvert post-copulatory choice and females need not benefit from polyandry if they cannot control their number of sexual 'partners'.

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Figure 1. (a) A colorful *Poecilia latipinna* male courts a lecithotrophic female (Don DeMaria). (b) A drab *Heterandria formosa* male with long gonopodium (Pierson Hill). (c) A male with gonopodium swung forward approaches a matrotrophic *Heterandria* female (Chiara Sciarone).

Figure 2. Matrotrophy and superfetation can originate from shifts in the timing of fertilization. (a) An ancestral lecithotrophic species provisions oocytes before fertilization (blue line). Fetal development (dotted red line) continues without further increase in weight. (b) Eggs are fertilized before they are fully provisioned. As a result, provisioning continues after fertilization (matrotrophy) and the next litter is conceived before birth of the previous litter (superfetation). (c) Figure 2. Matrotrophy and superfetation can originate from shifts in the timing of fertilization. (a) An ancestral lecithotrophic species provisions oocytes before fertilization (blue line). Fetal development (dotted red line) continues without further increase in weight. (b) Eggs are fertilized before they are fully provisioned. As a result, provisioning continues after fertilization (matrotrophy) and the next litter is conceived before birth of the previous litter (superfetation). (c) Subsequent evolution results in multiple **small litters** with short interbirth intervals.